Genetic Correlations among Selected Traits in Canadian Holsteins

P. Martin[1,2*], C. Baes[1], K. Houlahan[1], C. M. Richardson[1], J. Jamrozik[1,3], and F. Miglior[1,3]

[1]Centre for Genetic Improvement of Livestock, Department of Animal Biosciences, University of Guelph, Guelph, ON

[2]Génétique Animale et Biologie Intégrative (GABI), Institut National de la Recherche Agronomique (INRA), AgroParisTech, Université Paris-Saclay, Jouy en Josas, France

[3]Canadian Dairy Network, Guelph, ON

[1]Corresponding author: paulinemartin@inra.fr

Abstract

In the Canadian dairy industry, there are currently over 80 traits routinely evaluated, and more are considered for potential selection. Particularly, in the last few years, recording has commenced for several new phenotypes required to introduce novel traits with high economic importance into the selection program. However, without a systematic estimation of the genetic correlations that exist among traits, the potential results of indirect selection are unknown. Therefore, twenty-nine traits representative of the trait diversity for first lactation Canadian animals were selected. Their two-by-two genetic correlations were estimated from a dataset of 62,498 first lactation Holstein cows, using a Markov Chain Monte Carlo Gibbs sampling approach. The general tendencies among the

groups of traits confirm that production traits are negatively correlated with fertility traits and that functional traits are positively correlated with one another. The association of udder depth with fertility and disease resistance has also been highlighted. This contribution offers a comprehensive overview of current estimates across traits and includes correlations with novel traits that constitutes an original addition to the literature. These new estimates can be used for newly developed genomic evaluation models and possibly leads to more accurate estimations of the dairy cows' overall genetic merit.

Key Words: Genetic correlations, Holstein

In order to be considered for selection in dairy cattle populations, a specific trait must have an economic value, sufficient genetic variability and heritability, be measurable at a low cost and be clearly and consistently recordable (Shook 1989). Historically, most selection programs have largely focused on milk production, with some emphasis on type traits, for their ability to meet this criteria through their high economic importance and systematic data recording (Miglior et al. 2017). However, strong genetic selection for production traits has resulted in unfavorable, indirect selection for reduced health and fertility, highlighting the existence of antagonistic genetic correlations among economically important traits (Miglior et al., 2017). Although large differences in magnitude exist among studies, there is a general unfavorable relationship reported between milk production and reproductive performance, (Veerkamp et al. 2001; Kadarmideen et al. 2003; Pryce et al. 2004; Melendez and Pinedo 2007) as well as between milk production and health traits (Simianer et al. 1991; Kadarmideen et al. 2000). These results further confirm the importance of considering genetic correlations when selecting for multiple traits. Weigel et al. (2017) defined these correlations by how the genetic superiority for one trait tends to be inherited with genetic superiority or inferiority for another trait. The cause of a genetic correlation may be found at the genomic level, due to linkage or pleiotropy among the regions influencing the considered traits (Rauw et al. 1998). Therefore, estimates of genetic correlations are specific to the population under selection as they are influenced by the allele frequencies of that population (Falconer and Mackay 1996).

Currently, there are over 80 traits routinely evaluated by the Canadian Dairy Network (Guelph, ON; https://www.cdn.ca/). The introduction of genomic selection, and the development of additional recording systems and proxies, has permitted the evaluation of new traits that were previously too challenging to be recorded in the overall population. This contributed to, and even

accelerated, the availability of traits under consideration for selection. To improve the selection process and prepare for potential inclusion of novel traits such as feed efficiency and methane emission in the composite national indexes, it is imperative to complete a systematic evaluation of the genetic correlations between current and novel traits. If some genetic correlations have been previously estimated for Canadian Holstein, most of them remain unknown. The objective of this paper was to estimate the missing correlations among traits of interest.

MATERIALS AND METHODS

Choice of Traits

An evaluation of the genetic correlations between over 80 traits is computationally demanding and complex, therefore, a selection was made among the traits. To avoid the multiplication of traits, the first level of composite trait was used for conformation traits instead of each individually recorded trait, with the exception of udder depth considering its importance in the selection objective. Our analysis was limited to first parity cows to take advantage of the existing literature that mostly focus on primiparous animals. This resulted in removal of disease traits that have a low occurrence in first lactation, such as milk fever. Finally, a few traits were not included due to their nature of not being suitable for correlation estimation in our case (longevity traits, for instance, as we consider only first lactation animals). Overall, 29 of the 80 traits were selected.

Trait Definitions

Production traits investigated were milk yield (**MY**), protein yield (**PY**), fat yield (**FY**), protein percent (**P%**) and fat percent (**F%**) and were expressed on a 305-day lactation basis. Udder depth (**UD**) was defined as a score ranging from 1 to 9, with an intermediate optimum, while other type traits, mammary system (**MS**), feet and legs (**FL**), dairy strength (**DS**) and rump, were

composite traits ranging from 40 to 97. The exact definition of the conformation phenotypes can be found on the Holstein Canada website (https://www.holstein.ca/Public/en/Services/Classification/Breakdown_of_Traits). Fertility traits were split into two categories: those involving fertility prior to first calving, referred to as "heifer" and those involving fertility during the first lactation, referred to as "cow". Heifer fertility traits included age at first service (**AFS**), 56-day non-return rate (**NRR**) (0=back in heats, 1=pregnant), and the interval from first service to conception (**FSTC**). Cow fertility traits included the interval from calving to first service (**CTFS**), NRR, FSTC, and days open (**DO**). Milking speed (**MSP**) and milking temperament (**MT**) were defined as a score ranging from 1 (very slow / very nervous) to 5 (very fast / very calm). Calving ease (**CE**) was defined as a score ranging from 1 (unassisted or unobserved calving) to 4 (caesarean). Calf survival (**CS**) was defined as 0 = stillborn within the first 24h and 1 = alive. The somatic cell score (**SCS**) was calculated from the test-days occurring in the first 150 days of lactation. Only animals with at least three different measures were retained and the cell counts (**SCC**) of the different test-days were averaged before being log-transformed to SCS using the formula SCS = $\log_2$ (SCC/100 000) +3. Health disorders, clinical mastitis (**CM**), displaced abomasum (**DA**), ketosis, metritis, retained placenta (**RP**), cystic ovaries (**CO**) and lameness were defined as binary traits, where 0 = no case, and 1 = at least one case. An animal was considered sick if a health event was recorded during the first 305 days after calving.

Population Resources and Phenotypes

Phenotypic data was extracted from the Canadian Dairy Network (Guelph, ON) database. Holstein cows that calved for the first time from 2000 onwards and had a phenotype for every trait (with the only possible exception of health traits) were considered. A minimum of 50 cows from the same herd was required. The health dataset provided by the Canadian Dairy Network contained

historically recorded health (disease) events; however, event recording was not consistent across herds or years. Not all the herds started health data recording at the same time and some of them record only partial information (only mastitis events, for instance). To deal with this heterogeneity of recording, only herds with at least one health event recorded were selected. Then, to distinguish between missing information and healthy animals, we considered that the cow was healthy if at least one health event (other than mastitis) was recorded in the herd during the calving year. Otherwise, the phenotype was considered missing. The final dataset (after edits) consisted of 62,498 cows from 663 herds and 53,711 cows from the same herds for health data. The number of cows for the health data set is smaller as recording of health traits started only after 2006.

Pedigree was traced as far back as possible, resulting in a pedigree file with 319,299 animals. Animals with performances came from 5,423 different sires. Animals not related to others were discarded.

Models and Analyses

Among all considered correlations, 128 of 406 were found in Canadian literature, from 12 different sources (Miglior et al., 2007; Loker et al., 2009; Thomas, 2011; Koeck et al., 2012a; b, 2013a; b, 2015a; b; Jamrozik et al., 2013, 2016; Jamrozik and Kistemaker, 2016). Most of the correlations were only calculated once, with a few of them found in two different articles. Three correlations (between CM and somatic cell score (**SCS**), between DA and ketosis and between metritis and RP) were estimated in three different articles. As these correlations were previously estimated, they were not estimated as part of this work. The previously estimated correlations are reported in Supplementary material.

The correlations were estimated from covariance components using bi-variate linear animal models. Although threshold models are supposed to be more appropriate for binary traits,

it was decided, for a matter of homogenization among variable and with the Canadian literature, to use also linear models for binary and qualitative traits. Numerous studies have found indeed no improvement of using threshold models compared to linear models (e.g. Negussie et al. 2008).

The model considered for all traits can be expressed in matrix notation as:

$$y = Xb + Z_1h + Z_2a + e$$

where **y** is the vector of observations for the trait, **b** is the vector of fixed effects for the trait, **h** is the vector of random effects, **a** is the vector of animal additive genetic effects, **e** is the vector of residuals, and **X**, $\mathbf{Z_1}$ and $\mathbf{Z_2}$ are respective incidence matrixes assigning observations to effects. Random effects were assumed to be normally distributed with means equal to zero and covariance structure equal to

$$Var\begin{pmatrix} h \\ a \\ e \end{pmatrix} = \begin{pmatrix} I_h \otimes H & 0 & 0 \\ 0 & G \otimes A & 0 \\ 0 & 0 & I_r \otimes R \end{pmatrix}$$

Where **G** is a (co)variance matrix of random direct additive genetic effects, **R** is the residual (co)variance matrix and **H** is the (co)variance matrix of a potential additional random effect to that specific trait. The **A** matrix represents the additive genetic relationships among animals, and $\mathbf{I_h}$ and $\mathbf{I_r}$ are identity matrices which have orders equal to levels of appropriate random genetic and residuals effects.

The environmental effects included in the various models were chosen to emulate those from the routine national evaluation models considering the specificities of our sampled population. Fixed and random effects including in each model for the various analyzed traits can be found in Table 1.

Variance components were estimated using a Markov Chain Monte Carlo (MCMC) Gibbs sampling approach with the RJMC procedure within the DMU package (Madsen and Jensen 2008). The total length of the Gibbs chain was 2,000,000, with a burn-in of 200,000. Flat prior distribution was assumed for fixed and random effects and an inverted Wishart distribution was assumed for variance component estimation. Estimates from a preliminary study performed on a subset of the dataset were used as priors for variance components. The conservative burn-in period was determined based on trace plots of selected covariance components, tested with various priors. This was sufficient to minimize the influence of a potential lack of accuracy from the priors.

Estimates of genetic correlations were calculated as posterior means of all samples after burn-in. The statistical significance of point estimates was determined using an approximated 95% Bayesian credible interval, by determining whether 0 was included in the interval or not. The interval was obtained by excluding the 2.5% more extreme samples of each side from the posterior distribution. Independent numbers of samples were estimated using the method of initial monotone sequence estimator (Geyer 1992).

As a validation of correlations estimated in the current study, two correlations that were already estimated in the literature from Canadian data were re-estimated using the dataset and methods presented in this paper. These two correlations were the correlation between MY and FY and the correlation between CTFS and FSTC.

The complete correlation matrix (i.e. including both estimated correlations and correlations from the Canadian literature) was checked with the R software (R Development Core Team 2005) and appropriate bending was applied to make it positive definite following Schaeffer's method (Schaeffer 2014). Briefly, this method starts from the equation

$$G=UDU'$$

with G being the correlation matrix and D having the eigenvalues of G on its diagonal. Some appropriate corrections are performed on the negative eigenvalues to make them positive, based on the square of the sum of their value and the lowest positive eigenvalue. Then the correlation matrix is reconstructed using the modified D.

RESULTS AND DISCUSSION

Descriptive Statistics

Descriptive statistics for the analyzed traits, post editing, are presented in Table 2. Restrictions on herd size and ensuring each animal had a phenotype for all analyzed traits likely introduced a slight bias. The animals selected for this study had slightly higher production levels than the average animal. Some differences were observed in the fertility traits, with animals selected for this study being bred earlier (at a younger age and/or sooner after calving) than the population average. This difference in fertility traits is not surprising, as the animals selected for this study were from large herds that recorded phenotypes for all traits. These large herds are often associated with high adoption of new technologies and specific attention allocated to reproductive performance. Another point about the data is that only animals phenotyped on all traits were kept in the study. By doing this, we did not only discard herds with partial phenotyping, but also all animals that were culled before the end on the observation period because of poor health or poor fertility. For this reason, we have introduced another bias in the analyses that may have influenced the results of the correlation estimations.

There was no difference between the selected animals and the population average for workability or type traits. Frequencies observed for health traits, with the exception of CM, were lower than those reported by Koeck et al. (2012b), where mean disease frequencies of 12.6 (CM), 3.7 (DA), 4.5 (ketosis), 4.6 (RP), 10.8 (metritis), 8.2 (CO) and 9.2 (lameness), were observed. This

suggests that some missing data may have been taken for healthy animals despite our data validation.

Estimated Correlations

The genetic correlations estimated in this study are presented in Table 3 to Table 6. The complete matrix, including genetic and residual correlations when estimated, is available in Supplementary Table 1.

Correlations between production traits and all other traits are presented in Table 3. Previous Canadian studies estimated the correlations between MY and other production traits (Supplementary Table 1). These literature estimates were similar to other studies (Dematawewa and Berger 1998; Mokhtari et al. 2015; Frioni et al. 2017; Gibson and Dechow 2018). Fat yield and F% were favorably correlated (0.38), while other correlations among FY and PY with F% and P% were close to 0 (between -0.1 and 0.1). This pattern follows those found in previous studies (Boichard and Bonaïti 1987; Lembeye et al. 2016).

Genetic correlations between yield and type traits were previously estimated in Canadian literature (Supplementary Table 1), however, correlations between F% and P% with type traits were estimated in the current study. These estimates for F% and P% with type traits were less than 0.20, ranging from 0.15 (UD with P%) to -0.03 (FL with P%), the correlations between the milk contents and UD and MS being the only ones significant. Previous Canadian literature found no correlation between production yields and FL, and favorable correlations between production yields with DS and MS. These estimates are in concordance with results between type traits and production traits recently estimated in US Brown Swiss cattle (Gibson and Dechow 2018).

Correlations between yield traits and heifer fertility traits (-0.24 to -0.13 for NRR and 0.01 to 0.28 for FSTC) were weak and unfavorable, i.e. higher yields were correlated to lower NRR and longer FSTC. Estimates between production yields and cow fertility traits were low with correlations near zero. However, correlation estimates between production yields and DO, a trait that accounts for several components of cow fertility, were significantly unfavorable (0.18 to 0.21). This unfavorable correlation between production and fertility is well-known and has been previously discussed (Andersen-Ranberg et al. 2005; Abe et al. 2009; Mokhtari et al. 2015; Frioni et al. 2017; Gibson and Dechow 2018). Some authors have pointed out that the evidence of a strong antagonist association between milk production and reproductive performance is open to criticism due to physiological and management factors that are not taken into account in the analyses (Bello et al. 2012; LeBlanc 2013). Correlations between production traits and CE were unfavorable (around 0.20 and significant for the yield traits and around 0.05 and not significant for the contents), in accordance with estimates found by Eaglen et al. (2013).

Correlations between production traits with MSP and MT estimated in this study were near zero (-0.10 to 0.07), and in the same range as previously found by Gibson and Dechow (2018). A correlation of 0.39 between CM and MY, found through analysis of Canadian literature, is in the range reported in reviews by Rupp and Boichard (2003) and Martin et al. (2018). Previous Canadian literature also provides detail on the correlations between production traits and diseases, such as DA, RP, CO, ketosis, metritis and lameness. Generally, production traits were favorably correlated with ketosis and metritis and almost uncorrelated with DA and RP. Milk yield was unfavorable correlated with CO and lameness.

Table 4 presents correlations of type traits with the remaining traits. Udder depth had a strong positive correlation with MS (0.80), which was expected considering UD is included in the

calculation of MS. Udder depth had a slightly negative correlation with other type traits (-0.17 to 0.09). The correlations between type traits and MS are close to zero (-0.06 to 0.08).

Udder depth was found to be favorably correlated with all fertility traits. Other type traits such as FL, DS and rump were favorably correlated with heifer fertility, while unfavorably corelated with cow fertility. Correlations between fertility and MS were, however, close to zero. These results follow previous work done on the associations between type traits and fertility traits (Zink et al. 2011; Gibson and Dechow 2018).

Milking speed was found favorably correlated with both MS (0.17) and UD (0.14), in line with current literature (Wiggans et al. 2007; Gibson and Dechow 2018). A favorable correlation (-0.15) was also found between UD and resistance to various disease (DA, ketosis and CO), which could indicate shallow udders are genetically correlated with lower incidence of disease. Feet and legs score was favorably correlated with lameness (-0.46), and DS was unfavorably associated with displaced abomasum (0.26). The unfavorable correlation between DS and displaced abomasum was also found by Dechow et al., (2004). All the correlations reported in this paragraph were significantly different from 0.

Correlations between reproduction traits, workability traits and health traits are presented in Table 5. Days open ranged in correlation with other reproduction traits from -0.20 for NRR in cow to 0.88 for FSTC in cow. However, only the correlations of DO with its components (CTFS and FSTC), which were both above 0.8, were significant. Other studies have estimated correlations between various measures of fertility (e.g. Veerkamp et al., 2001; Andersen-Ranberg et al., 2005; Abe et al., 2009; Mokhtari et al., 2015). Although the phenotypes considered in these studies are diverse and no direct comparison can be made; the general trends are consistent with those found in this study. Unfavorable correlations were observed between CM and the three heifer fertility

traits: AFS (-0.04), NRR (0.20) and FSTC (-0.41), only the last one being significantly different from 0. The direction is the same in the Canadian literature for the correlations between these fertility traits and SCS. This could indicate that heifers who become pregnant at a younger age may be genetically predisposed to having mastitis. The opposite was observed for correlations between CM and SCS with cow fertility, where the correlations were favorable (0.29, -0.19 and 0.20 for the correlation between CM and CTFS, NRR and FSTC respectively) but not significant due to their large credible intervals. This is one of the rare cases where we seems to have such a difference between heifer and cow fertility traits in their correlations with other traits. Even though they were not always significant, correlations of heifer and cow fertility traits with production traits or UD and MS showed the same trend, for example. Nevertheless, mastitis often occurs around calving time or in early lactation, the same periods when cow fertility is challenged. Heifers and cows are not facing the same biological needs at the reproduction time, as cows are just recovering from calving while heifers are not. It is therefore not surprising that correlations with CM and SCS are in the opposite direction between cows and heifers. The difference of trend observed for the correlation with RP tends to confirm this hypothesis, even though these correlations are not significant.

Estimates of correlations between workability traits, calving traits, and health traits are presented in Table 6. Workability traits were strongly positively correlated (0.58, significant). This indicates that cows with a genetically faster MSP also seem to have a calmer MT. However, this tendency was also slightly correlated with a higher risk of CM and SCS (significant correlations around 0.2). The relationship between MSP with SCS and CM has been previously analyzed in various studies and confirms the association found here (Boettcher et al., 1998; Rupp and Boichard, 1999; Zwald et al., 2005 for SCS; Govignon-Gion et al., 2012; Pérez-Cabal and

Charfeddine, 2013 for CM). Some studies, however, found evidence that animals with low MSP may be more susceptible to CM (Lund et al. 1994; Rupp and Boichard 2003). Moreover, Samoré and Groen (2010) found a nonlinear relationship between EBV for SCS and MSP. This suggests that the relationship between MSP and CM traits may not be simply linear and requires more investigation. Slight associations were found between workability traits and other disease traits, all less than 0.20 in magnitude. Genetically, fast milking animals appear to be significantly more resistant to RP (-0.17) and CO (-0.15). Calm milking temperament appears slightly but significantly genetically correlated with less lameness (-0.07).

Some significant correlations were also observed between calving traits and health traits, such as difficult calving being associated with DA (0.18), or stillborn calves being associated with RP (-0.62). It is known from the literature that cases of RP occur around calving, and that almost all cases of DA occur during the first 100 days of lactation (Zwald et al. 2004; Koeck et al. 2012a). In early lactation, cows have large physiological demands while going through various transitional changes (Sordillo et al. 2009). At this time, cows are in a negative energy balance and metabolic diseases may follow as a consequence of a severe and prolonged period of time in this state (Collard et al. 2000).

Accuracy of the Estimates

Among all the Gibbs sampling analyses, the number of independent samples for genetic correlations ranged from 182 to 7,213, with an average of 738 and a standard deviation of 1103. The number of independent samples varied among traits, with the highest numbers being found for production traits and the lowest for fertility traits. These numbers were in the same range as some previously mentioned in the literature (Steinbock et al. 2003; Jamrozik et al. 2005).

As we previously mentioned, two correlations that were already estimated in the literature from Canadian data were re-estimated in this study for validation purposes. A correlation of 0.76 with a 95% Bayesian credible interval of [0.75; 0.77] between milk yield and fat yield and a correlation of 0.47 [0.21; 0.71] between calving to first service and first service to conception in cow, were determined. These values are a slightly higher than Canadian estimates from the literature, 0.57 and 0.31, respectively. If the difference between the literature and the correlations estimated in the current study for calving to first service and first service to conception is not significant, the correlation estimated by Miglior et al. (2007) for milk yield and fat yield does not fall into our posterior interval. This slight gap may be explained by differences between the two datasets. Analysis in Miglior et al. (2007) was performed on test day records from Holstein cows only in the province of Quebec. The dataset for this study was a sample of Holstein cows across Canada that considered a 305-day lactation. Both values are in the range of what was found in the literature (Boichard and Bonaïti 1987; Dematawewa and Berger 1998; Mokhtari et al. 2015; Lembeye et al. 2016; Gibson and Dechow 2018).

The size of the interval was highly variable, depending on the traits considered. It ranged from 0.04 among production traits to 1.42 between NRR (heifer) and lameness. These results were in the same ranges and sometimes slightly higher than what was found in literature (Jamrozik et al. 2005; Abe et al. 2009; Zink et al. 2011; Koeck et al. 2012a, 2013b; Mokhtari et al. 2015; Jamrozik et al. 2016). The magnitude of the credible intervals for some correlations made these results difficult to interpret. Several factors can influence the accuracy of genetic correlation estimation. Accuracy is dependent on the dataset including sample size, quality of phenotyping, and repeated measures. The models used, and the nature of the traits themselves also have influence on the accuracy of the prediction. For these reasons, Falconer and Mackay (1996)

observed that estimates of genetic correlations are usually subject to large sampling errors. In the current study, the less accurate estimations were found between fertility traits and health traits. Fertility traits have a very low heritability (Jamrozik and Kistemaker 2016) and health traits, despite careful editing criteria, probably contain recording errors. Moreover, incidences of disease were low when compared to the number of animals in the population. This may explain why accuracy was low for those traits. Even though the estimates have large intervals, these correlations have never been estimated before from Canadian data and represent important information.

Considering that we used a 95% credible interval to determine the possible range of the correlation real value, there is, by definition, a 5% chance that the true correlation is outside this interval. As no less than 278 correlations were estimated in the current study, it could be expected that around 14 correlations are outside the credible interval that was predicted.

Considered in its entirety –i.e. including the estimates from the Canadian literature (Supplementary Table 1), the correlation matrix was of rank 29 and was not positive definite, as six eigenvalues were negative. Correlation matrices calculated from a single sample are supposed to be positive definite. In our case, the matrix is a patchwork of values coming from different sources and it is therefore not surprising that negative eigenvalues are present. Following the method of Schaeffer (2014), the matrix was transformed to become positive definite. This corrected matrix is presented in Supplementary Table 2. Overall, the uncorrected and the corrected matrices were very similar, with a Pearson correlation of 0.99 between them, and the average absolute difference being 0.02 ± 0.03.

CONCLUSIONS

This study focused on estimating correlations among selected traits for the Canadian Holstein cattle population. Correlations that were not previously reported in Canadian literature over the past ten years between the selected traits were estimated. This study provides correlations that have not previously been estimated and will be used specifically in applications of selection index studies, breeding strategies, and estimated response of selection. Future work using multiple trait models with more than two traits at a time may provide more accurate estimates to be used for selection programs.

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Table 1 Fixed and random effects fitted in the genetic parameter estimation for various trait groups

	Fixed Effects									*Random Effect*
	Herd - year - season	Age and region at calving	DIM2 at test day	Sex of calf	Herd-classification round-classifier	Stage of lactation-age at calving	Region - birth year - birth month	Age at prev. calving-month of 1st insemination	Age at prev. calving–month of prev. calving	Herd-year of birth
Production Traits (MY, FY, PY, F%, P%)	+	+	-	-	-	-	-	-	-	-
Type Traits (UD, MS, FL, DS, Rump)	-	-	-	-	+	+	-	-	-	-
Heifer Fertility Traits (AFS, FSTCh, NRRh)	-	-	-	-	-	-	+	-	-	+
CTFS	-	-	-	-	-	-	+	-	+	+
Other Cow Fertility Traits (NRRc, FSTCc, DO)	-	-	-	-	-	-	+	+	-	+
Workability Traits (MSP, MT)	+	+	+	-	-	-	-	-	-	-
Calving Traits (CE, CS)	+	+	-	+	-	-	-	-	-	-
Health Traits (CM, SCS, DA, Ketosis, Metritis, RP, CO, Lameness)	+	+	-	-	-	-	-	-	-	-

Note: A + indicated the inclusion of the effect in the model and a – indicates the effect was not included in the model.
DIM: days in milk, MY: milk yield, FY: fat yield, PY: protein yield, F%: fat percent, P%: protein percent, UD: udder depth, MS: mammary system, FL: feet and legs, DS: dairy strength, AFS: age at first service, NNR: 56-day non-return rate, FSTC: first service to conception, CTFS: calving to first service, DO: days open, MSP: milking speed, MT: milking temperament, CE: calving ease, CS: calf survival, CM: clinical mastitis, SCS: somatic cell score, DA: displaced abomasum, RP: retained placenta, CO: cystic ovaries

Table 2. Descriptive statistics of analyzed data for first lactation Holstein cows

Trait	Number of records	Mean	Standard Deviation	Minimum	Maximum
Milk (kg)	62,498	9,000.17	1,455.10	5,677	12,629
Fat (kg)	62,498	341.34	56.57	213	482
Protein (kg)	62,498	288.06	43.15	187	392
Fat Percent (%)	62,498	3.82	0.44	2.81	4.90
Protein Percent (%)	62,498	3.21	0.19	2.79	3.69
Udder Depth (points)	62,498	4.95	1.38	1	9
Mammary System (score)	62,498	79.45	4.99	40	89
Feet and Legs (score)	62,498	79.16	5.04	40	89
Dairy Strength (score)	62,498	81.15	3.83	40	93
Rump (score)	62,498	81.02	5.33	40	91
Age at First Service (days)	62,498	465.16	48.02	365	606
Non-Return Rate Heifer (0/1)	62,498	0.71	0.46	0	1
First Service to Conception Heifer (days)	62,498	18.16	32.57	0	145
Calving to First Service (days)	62,498	76.21	19.66	43	142
Non-Return Rate Cow (0/1)	62,498	0.57	0.49	0	1
First Service to Conception Cow (days)	62,498	25.09	33.35	0	127
Days Open (days)	62,498	102.12	37.58	48	214
Milking Speed (points)	62,498	3.09	0.73	1	5
Milking Temperament (points)	62,498	3.26	0.78	1	5
Calving Ease (points)	62,498	1.56	0.69	1	4
Calf Survival (0/1)	62,498	0.89	0.32	0	1
Clinical Mastitis (0/1)	53,711	0.13	0.34	0	1
Somatic Cell Score (score)	62,498	2.01	1.28	0.11	5.96
Displaced Abomasum (0/1)	53,711	0.03	0.16	0	1
Ketosis (0/1)	53,711	0.02	0.15	0	1
Metritis (0/1)	53,711	0.05	0.22	0	1
Retained Placenta (0/1)	53,711	0.04	0.19	0	1
Cystic Ovaries (0/1)	53,711	0.05	0.22	0	1
Lameness (0/1)	53,711	0.07	0.26	0	1

Table 3. Genetic correlations for the estimated production traits with all the other traits (with the 95% Bayesian credible interval in square brackets and correlations significantly different from 0 in bold)

	MY	FY	PY	F%	P%
F%	-	**0.38** [0.36 ; 0.40]	**-0.10** [-0.12 ; -0.07]	-	-
P%	-	**0.08** [0.06 ; 0.10]	**0.07** [0.05 ; 0.09]	-	-
UD	-	-	-	**0.09** [0.05 ; 0.12]	**0.15** [0.12 ; 0.19]
MS	-	-	-	**0.08** [0.05 ; 0.13]	**0.07** [0.02 ; 0.11]
FL	-	-	-	0.04 [-0.04 ; 0.13]	0.04 [-0.04 ; 0.12]
DS	-	-	-	0.03 [-0.01 ; 0.08]	-0.03 [-0.07 ; 0.01]
Rump	-	-	-	-0.01 [-0.05 ; 0.04]	0.00 [-0.04 ; 0.05]
AFS (heifer)	-	-	-	0.01 [-0.11 ; 0.10]	**-0.12** [-0.22 ; -0.03]
NRR (heifer)	-0.20 [-0.41 ; 0.00]	-0.13 [-0.34 ; 0.09]	**-0.24** [-0.45 ; -0.04]	0.12 [-0.08 ; 0.34]	0.09 [-0.09 ; 0.27]
FSTC (heifer)	**0.23** [0.01 ; 0.47]	0.01 [-0.24 ; 0.26]	**0.28** [0.05 ; 0.51]	**-0.30** [-0.51 ; -0.10]	-0.07 [-0.27 ; 0.14]
CTFS (cow)	-	-	-	-0.02 [-0.13 ; 0.10]	**-0.15** [-0.26 ; -0.04]
NRR (cow)	-0.07 [-0.26 ; 0.12]	-0.02 [-0.22 ; 0.17]	**-0.21** [-0.40 ; -0.04]	0.06 [-0.12 ; 0.22]	**-0.20** [-0.37 ; -0.05]
FSTC (cow)	0.05 [-0.15 ; 0.25]	-0.04 [-0.25 ; 0.16]	0.11 [-0.10 ; 0.29]	-0.06 [-0.24 ; 0.12]	0.13 [-0.05 ; 0.30]
DO (cow)	**0.18** [0.06 ; 0.30]	**0.18** [0.05 ; 0.30]	**0.21** [0.09 ; 0.33]	-0.01 [-0.12 ; 0.10]	0.03 [-0.08 ; 0.13]
MSP	**0.06** [0.02 ; 0.10]	**0.07** [0.04 ; 0.11]	**0.06** [0.02 ; 0.09]	0.03 [-0.01 ; 0.06]	-0.01 [-0.04 ; 0.02]
MT	-	-	-	-0.05 [-0.09 ; -0.01]	-0.04 [-0.07 ; 0.00]
CE	**0.19** [0.12 ; 0.26]	**0.22** [0.15 ; 0.29]	**0.21** [0.14 ; 0.28]	0.06 [0.00 ; 0.14]	0.04 [-0.03 ; 0.10]
CS	-0.03 [-0.14 ; 0.07]	**-0.11** [-0.21 ; -0.01]	-0.08 [-0.18 ; 0.02]	**-0.11** [-0.20 ; -0.01]	-0.09 [-0.18 ; 0.00]
CM	-	**-0.11** [-0.20 ; -0.02]	-0.03 [-0.12 ; 0.06]	**-0.12** [-0.21 ; -0.03]	-0.03 [-0.11 ; 0.06]
DA	-	-	-	-0.02 [-0.11 ; 0.07]	-0.06 [-0.15 ; 0.02]
Ketosis	-	-	-	-0.01 [-0.09 ; 0.07]	**-0.17** [-0.25 ; -0.10]
Metritis	-	-	-	-0.03 [-0.07 ; 0.01]	-0.04 [-0.08 ; 0.00]
RP	-	-	-	0.02 [-0.08 ; 0.13]	0.00 [-0.09 ; 0.10]
CO	-	-	-	-0.02 [-0.13 ; 0.08]	**-0.16** [-0.26 ; -0.07]
Lameness	-	-	-	-0.01 [-0.05 ; 0.03]	**-0.07** [-0.10 ; -0.03]

Note: MY: milk yield, FY: fat yield, PY: protein yield, F%: fat percent, P%: protein percent, UD: udder depth, MS: mammary system, FL: feet and legs, DS: dairy strength, AFS: age at first service, NNR: 56-day non-return rate, FSTC: first service to conception, CTFS: calving to first service, DO: days open, MSP: milking speed, MT: milking temperament, CE: calving ease, CS: calf survival, CM: clinical mastitis, DA: displaced abomasum, RP: retained placenta, CO: cystic ovaries

Table 4. Genetic correlations for the estimated type traits with all remaining traits (with the 95% Bayesian credible interval in square brackets and correlations significantly different from 0 in bold)

	UD	MS	FL	DS	Rump
MS	**0.80** [0.76 ; 0.83]				
FL	**-0.17** [-0.27 ; -0.07]	-0.06 [-0.19 ; 0.07]			
DS	**-0.10** [-0.16 ; -0.04]	0.08 [0.00 ; 0.15]	**0.32** [0.21 ; 0.43]		
Rump	**-0.09** [-0.16 ; -0.03]	0.00 [-0.08 ; 0.08]	0.05 [-0.07 ; 0.18]	**0.32** [0.24 ; 0.38]	
AFS (heifer)	-0.01 [-0.12 ; 0.11]	0.06 ['-0.08 ; 0.21]	-0.02 [-0.20 ; 0.17]	**-0.26** [-0.39 ; -0.13]	-0.14 [-0.28 ; 0.00]
NRR (heifer)	0.15 [-0.07 ; 0.38]	0.05 [-0.20 ; 0.31]	0.12 [-0.16 ; 0.42]	0.23 [0.00 ; 0.48]	**0.35** [0.13 ; 0.57]
FSTC (heifer)	-0.17 [-0.41 ; 0.09]	-0.09 [-0.36 ; 0.21]	-0.24 [-0.52 ; 0.10]	-0.15 [-0.40 ; 0.12]	-0.26 [-0.50 ; 0.03]
CTFS (cow)	**-0.22** [-0.33 ; -0.10]	-0.07 [-0.22 ; 0.08]	-0.11 [-0.29 ; 0.08]	**0.35** [0.21 ; 0.49]	0.14 [-0.01 ; 0.29]
NRR (cow)	**0.19** [0.01 ; 0.40]	0.15 [-0.06 ; 0.39]	**-0.36** [-0.58 ; -0.12]	-0.11 [-0.31 ; 0.10]	0.02 [-0.19 ; 0.25]
FSTC (cow)	**-0.25** [-0.45 ; -0.04]	-0.14 [-0.36 ; 0.11]	**0.30** [0.04 ; 0.55]	**0.40** [0.18 ; 0.64]	0.10 [-0.11 ; 0.35]
DO (cow)	**-0.13** [-0.25 ; -0.01]	-0.02 [-0.16 ; 0.14]	0.14 [-0.04 ; 0.35]	**0.47** [0.33 ; 0.62]	**0.17** [0.02 ; 0.32]
MSP	**0.14** [0.09 ; 0.20]	**0.17** [0.08 ; 0.21]	0.07 [-0.05 ; 0.20]	-0.06 [-0.13 ; 0.01]	**-0.09** [-0.17 ; -0.02]
MT	0.01 [-0.05 ; 0.07]	0.03 [-0.06 ; 0.11]	0.02 [-0.12 ; 0.15]	0.00 [-0.08 ; 0.07]	0.03 [-0.05 ; 0.11]
CE	**-0.12** [-0.23 ; -0.03]	-0.05 [-0.18 ; 0.07]	0.09 [-0.10 ; 0.25]	0.05 [-0.07 ; 0.16]	0.13 [0.00 ; 0.24]
CS	-0.10 [-0.23 ; 0.01]	-0.06 [-0.21 ; 0.08]	0.05 [-0.15 ; 0.22]	0.14 [0.00 ; 0.27]	0.11 [-0.04 ; 0.25]
CM	-	-0.12 [-0.27 ; 0.02]	0.05 [-0.18 ; 0.27]	0.10 [-0.04 ; 0.24]	0.06 [-0.08 ; 0.21]
SCS	-	**-0.29** [-0.38 ; -0.20]	0.03 [-0.12 ; 0.17]	0.05 [-0.04 ; 0.13]	0.01 [-0.09 ; 0.10]
DA	**-0.15** [-0.27 ; -0.05]	**-0.18** [-0.31 ; -0.04]	0.05 [-0.13 ; 0.23]	**0.26** [0.13 ; 0.38]	0.12 [-0.02 ; 0.25]
Ketosis	**-0.15** [-0.26 ;-0.04]	**-0.16** [-0.31 ; -0.02]	-0.14 [-0.35 ; 0.08]	0.01 [-0.12 ; 0.14]	0.06 [-0.09 ; 0.20]
Metritis	0.05 [-0.01 ; 0.12]	0.02 [-0.07 ; 0.11]	-0.08 [-0.23 ; 0.07]	-0.05 [-0.13 ; 0.03]	-0.07 [-0.16 ; 0.02]
RP	0.14 [0.00 ; 0.26]	0.13 [-0.03 ; 0.29]	-0.07 [-0.27 ; 0.14]	-0.06 [-0.20 ; 0.09]	0.00 [-0.16 ; 0.15]
CO	**-0.15** [-0.28 ; -0.02]	-0.13 [-0.28 ; 0.03]	-0.04 [-0.25 ; 0.18]	-0.02 [-0.17 ; 0.122]	0.13 [-0.03 ; 0.28]
Lameness	0.08 [0.01 ; 0.14]	0.00 [-0.10 ; 0.09]	-	-0.02 [-0.10 ; 0.07]	-0.02 [-0.11 ; 0.07]

Note: UD: udder depth, MS: mammary system, FL: feet and legs, DS: dairy strength, AFS: age at first service, NNR: 56-day non-return rate, FSTC: first service to conception, CTFS: calving to first service, DO: days open, MSP: milking speed, MT: milking temperament, CE: calving ease, CS: calf survival, CM: clinical mastitis, SCS: somatic cell score, DA: displaced abomasum, RP: retained placenta, CO: cystic ovaries

Table 5. Genetic correlations for the estimated fertility traits with all the remaining traits (with the 95% Bayesian credible interval in square brackets and correlations significantly different from 0 in bold)

	AFS	NNR (heifer)	FSTC (heifer)	CTFS	NRR (cow)	FSTC (cow)	DO
DO	0.17 [-0.03 ; 0.33]	0.14 [-0.13 ; 0.36]	0.10 [-0.18 ; 0.34]	**0.84** [0.74 ; 0.94]	-0.20 [-0.42 ; 0.05]	**0.88** [0.79 ; 0.95]	-
MSP	0.00 [-0.16 ; 0.15]	0.15 [-0.09 ; 0.36]	0.19 [-0.10 ; 0.46]	0.05 [-0.10 ; 0.22]	-0.10 [-0.31 ; 0.16]	0.02 [-0.25 ; 0.28]	0.09 [-0.07 ; 0.26]
MT	0.04 [-0.13 ; 0.21]	0.21 [-0.05 ; 0.44]	-0.10 [-0.36 ; 0.16]	0.18 [0.00 ; 0.38]	0.16 [-0.07 ; 0.43]	-0.15 [-0.42 ; 0.11]	0.05 [-0.13 ; 0.24]
CE	-	-	-	-	-	-	0.00 [-0.24 ; 0.25]
CS	-	-	-	-	-	-	-0.07 [-0.31 ; 0.19]
CM	-0.04 [-0.34 ; 0.25]	0.20 [-0.17 ; 0.58]	**-0.41** [-0.72 ; -0.02]	0.29 [0.00 ; 0.64]	-0.19 [-0.57 ; 0.24]	0.20 [-0.19 ; 0.58]	0.18 [-0.13 ; 0.54]
SCS	**-0.24** [-0.40 ; -0.08]	0.04 [-0.23 ; 0.28]	-0.07 [-0.35 ; 0.23]	0.17 [-0.01 ; 0.35]	0.08 [-0.17 ; 0.31]	**0.39** [0.10 ; 0.68]	**0.23** [0.05 ; 0.40]
DA	-	0.07 [-0.19 ; 0.33]	0.11 [-0.16 ; 0.39]	-	-0.28 [-0.52 ; -0.01]	**0.26** [0.01 ; 0.053]	0.21 [0.00 ; 0.43]
Ketosis	-	0.28 [-0.39 ; 0.78]	0.13 [-0.59 ; 0.78]	-	-0.53 [-0.88 ; 0.08]	-0.33 [-0.84 ; 0.32]	0.72 [-0.02 ; 0.96]
Metritis	-	-	0.51 [-0.10 ; 0.93]	-	-	0.36 [-0.31 ; 0.388]	0.53 [-0.15 ; 0.90]
RP	-	-	-0.25 [-0.54 ; 0.13]	-	-	0.18 [-0.13 ; 0.49]	0.14 [-0.12 ; 0.42]
CO	-	-	0.03 [-0.35 ; 0.43]	-	-	0.31 [-0.11 ; 0.77]	**0.34** [0.04 ; 0.70]
Lameness	-	-0.01 [-0.55 ; 0.51]	0.35 [-0.33 ; 0.90]	-	0.27 [-0.54 ; 0.88]	0.41 [-0.30 ; 0.90]	**0.80** [0.15 ; 0.98]

Note: AFS: age at first service, NNR: 56-day non-return rate, FSTC: first service to conception, CTFS: calving to first service, DO: days open, MSP: milking speed, MT: milking temperament, CM: clinical mastitis, SCS: somatic cell score, CE: calving ease, CS: calf survival, DA: displaced abomasum, RP: retained placenta, CO: cystic ovaries

Table 6. Genetic correlations for the estimated workability traits, calving traits and mammary health traits with the remaining traits (with the 95% Bayesian credible interval in square brackets and correlations significantly different from 0 in bold)

	MSP	MT	CE	CS	CM	SCS
MT	**0.58** [0.52 ; 0.63]	-	-	-	-	-
CE	-0.10 [-0.20 ; 0.00]	0.11 [-0.01 ; 0.22]	-	-	-	-
CS	-0.01 [-0.14 ; 0.12]	0.08 [-0.07 ; 0.22]	-	-	-	-
CM	**0.20** [0.06 ; 0.34]	**0.27** [0.13 ; 0.41]	-0.01 [-0.20 ; 0.19]	0.04 [-0.16 ; 0.24]	-	-
SCS	**0.22** [0.14 ; 0.29]	**0.11** [0.03 ; 0.19]	0.07 [-0.19 ; 0.06]	0.03 [-0.12 ; 0.17]	-	-
DA	0.08 [-0.05 ; 0.20]	0.04 [-0.09 ;0.16]	**0.18** [0.01 ; 0.35]	0.14 [-0.05 ; 0.32]	-	0.01 [-0.13 ; 0.15]
Ketosis	-0.04 [-0.16 ; 0.08]	-0.01 [-0.14 ; 0.11]	-0.12 [-0.32 ; 0.09]	-0.10 [-0.22 ; 0.21]	-	-0.04 [-0.18 ; 0.10]
Metritis	**0.08** [0.01 ; 0.15]	**0.08** [0.01 ; 0.15]	0.09 [-0.03 ; 0.22]	-0.07 [-0.24 ; 0.10]	-	0.04 [-0.06 ; 0.13]
RP	**-0.17** [-0.31 ; -0.03]	-0.09 [-0.23 ; 0.06]	-0.01 [-0.21 ; 0.21]	**-0.62** [-0.77 ; -0.44]	-	-0.06 [-0.22 ; 0.10]
CO	**-0.15** [-0.30 ; -0.01]	0.04 [-0.11 ; 0.19]	0.01 [-0.19 ; 0.23]	0.09 [-0.12 ; 0.31]	-	-
Lameness	0.04 [-0.03 ; 0.10]	**-0.07** [-0.14 ; -0.01]	0.01 [-0.11 ; 0.13]	-0.09 [-0.24 ; 0.07]	-	-

Note: MSP: milking speed, MT: milking temperament, CM: clinical mastitis, SCS: somatic cell score, CE: calving ease, CS: calf survival, DA: displaced abomasum, RP: retained placenta, CO: cystic ovaries